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ON THE APPENDAGES OF TREMATASPIS.

W. PATTEN.

IN a recent paper in the *American Naturalist*[1] on the structure of the Tremataspidæ, I maintained that the marginal openings (so-called gill openings) on the under surface of the head of Tremataspis might be interpreted as the points of attachment of metamerically arranged appendages. Whether all these appendages projected freely from the body like the jointed pectorals of Bothriolepis, or presented any one of the innumerable variations in structure and function to which such appendages might be subject, there was no means of determining. If one admits the extremely doubtful systematic position of the Ostracoderms, there is no satisfactory reason for calling the marginal openings of Tremataspis gill openings unless one assumes the whole point at issue by asserting that the Tremataspidæ are true vertebrates. But if the Tremataspidæ are provided with oar-like appendages, similar in structure and mode of attachment to those in other members of the Ostracoderms, such as Pterichthys and Bothriolepis, then these appendages must have been attached to the head, near the anterior end of the series of so-called gill openings. The anterior pair of incisions, or openings (of which I have found at least two additional pairs in front of the six pairs described by Rohon) are found on the lateral margin of the anterior part of the head, in precisely the position where the hypothetical oar-like appendages should be attached provided any were present. Moreover in Tolypaspis, Cyathaspis and Pteraspis, there is a very conspicuous rounded incision on the margin of the dorsal shield that has usually been regarded as the site of the lateral eyes, apparently because there was no other interpretation for these openings at hand, and because otherwise the lateral eyes would appear to be absent. But, these incisions also occur at points corresponding to the ones where the oar-like appendages in Pterichthys and Bothriolepis, and the anterior pair of incisions in Tremataspis, are located. The conclusion to be drawn from these facts is that Tremataspis, Cyathaspis, and Pteraspis were probably provided with jointed, oar-like swimming appendages similar in character and location to those of Pterichthys and Bothriolepis.

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[1] On the Structure and Classification of the Tremataspidæ. Vol. xxvii, No. 425, pp. 386 and 388.

Moreover, and this is the important point, if Tremataspis has a pair of jointed, armored appendages attached to the anterior margin of the ventral surface, they must have been attached to one of the *anterior pair* of marginal incisions. If this is the case, there is no escape from the conclusion that *behind* the oar-like appendages there are as many more pairs of serially homologous structures (but not necessarily similar to them in form or function) as there are pairs of marginal incisions.

The assumption that Trematapsis is provided with jointed pectorals is strengthened by the fact that Lindström[1] has described what he considers to have been an appendage in Cyathaspis. He states on p. 5: "Along with some other fragments was found, detached and broken into three pieces, what may be regarded as the shelly covering of an extremity or limb (Pl I, fig. 9–12). It is plain that it is not a fragment of the dorsal shield nor of one of the cornua. Its exterior ridged surface is, to wit, inflected towards the interior surface along the lateral edges and partly covers it. In all probability the muscular and other organs, which it has covered, were in the same way sheltered on both sides by similar plates. It is narrow, elongated, by degrees tapering and ending bluntly. The surface is of the same glossy lustre as the other portions of the exoskeleton and is covered with ridges which have a nearly parallel direction and continue without interruption. On the interior surface (Pl. I, Fig. 12) which is quite smooth, are seen the polygonal partition lines of the vacuole walls, and the openings of the minute canals. There is no evidence that it has consisted of more than one plate, nor that the supposed extremity has been covered by several plates, as the limbs of Pterichthys." Lindström does not attempt to justify his conclusion that the structure in question is an appendage, or to indicate its point of attachment, or the effect such a discovery, if confirmed, must have on the classification of the Ostracoderms. The importance of Lindström's discovery is somewhat diminished by the fact that what he calls an appendage is but a single plate. Hence it is uncertain whether it covered a small part only or the whole appendage, or whether it was part of a scale or spine paired or unpaired, belonging either to the head or trunk.

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[1] Lindström, G.: On Remains of a Cyathaspis, etc.: *Bihang J. K. Svenska Vet. Akads Handl* Bd. 21, Afd. IV. No. 3.

An examination of some beautiful specimens of Pteraspis in the British Museum indicates that the so-called lateral eye openings are better explained as points for the attachment of oar-like appendages, and that the projecting processes sometimes attached to the openings should be regarded, not as a portion of the matrix squeezed out of the orbits, but as either the remnants of an appendage itself, or as the matrix that originally filled the base of the appendage.

In view of the common bonds of relationship that unite the various groups of the Ostracoderms, and in view of the presence of at least one pair of jointed cephalic appendages in Bothriolepis, Pterichthys, and perhaps in Cyathaspis and Pteraspis, the presence of one or more appendages in Tremataspis appeared to be within the range of possibility. It remained to discover some traces of the appendages themselves.

Thus the matter stood at the time of writing in St. Petersburg, for the Imperial Academy of Sciences, my first paper on the Tremataspidæ.

On my return to America, I began work anew on a few fragments and isolated plates that had been obtained from Herr A. Simonson, on my visit to the island of Oesel, and to which I had previously failed to give adequate attention. One fragment of special importance was almost concealed in the rock and its true nature was not at first apparent; the other was similar to a plate first described by Rohon. When it became evident that these fragments were probably parts of appendages, it was too late to do more in that paper than refer to the fact that what appeared to be fragments of appendages of Tremataspis had been discovered.

I shall now describe what I consider to be the distal portion of an oar like appendage attached to the head of Tremataspis.

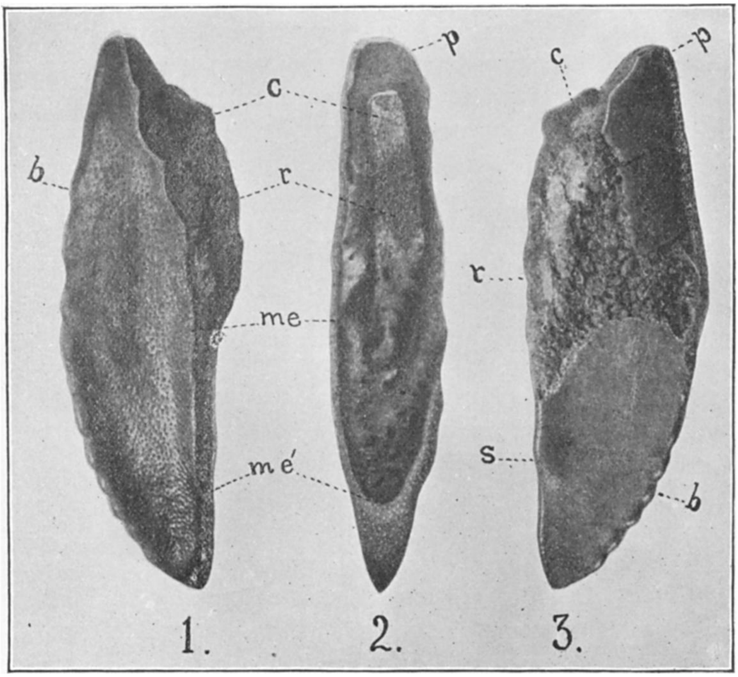

FIG. 1. Distal joint of cephalic appendage of Tremataspis seen from the ventral side. × 10.
FIG. 2. Same from median edge. × 10.
Fig. 3. Same from dorsal surface. × 10.
b. Beadings on margin. *c*. condyle. *m. e.* & *m. é.* rounded margin of polished layer. *p*. articular process. *r*. ridge. *s*. shoulder.

The structure, Figs. 1–3, was at first deeply imbedded in the matrix leaving only a small part of the dorsal surface exposed, from which the outer layers has been worn off, revealing the characteristic polygonal meshwork of the middle layer.

After exposing the entire dorsal surface of the plate by cautiously removing the matrix with fine needles, to insure against accidents in the subsequent treatment, it was photographed and modeled in wax on a large scale. This proved to be a wise precaution, as the extremely brittle and fragile plate, in spite of the utmost precaution, was accidentally injured, in one of the many occasions when it was being placed in position for examination. After the dorsal surface had been thoroughly studied, it was covered with hard balsam and fastened face downwards to a glass slide. When the remaining matrix had been removed and the balsam dissolved off, the completely isolated plate could be examined from any desirable point of view. The other plates to be described were treated in a similar manner.

When seen from what I consider to be the dorsal side, Fig. 3, the distal joint of the appendage appears something like the blade of a knife. It is about 2.5 mm. wide by 7.5 mm. long and of a light yellowish brown color. A cross section would be triangular, with the thickest part on what I assume to be the median side, or that side which when the appendage was in place was nearest the body. The opposite or lateral margin, especially toward its posterior end, is thinned down to a rather sharp edge, ornamented by a series of glistening beadings or scallops. Fig. 3*b*. The six beadings nearest the posterior end are the most regular and they are readily seen from either surface. Toward the anterior end of the lateral margin one can distinguish five or six more undulations, somewhat irregular in size and best seen from the under surface, Fig. 1, *b*. Towards its anterior end, the lateral margin becomes thicker and more rounded so that cross sections of the appendages at that point would be more oval in outline. The dorsal surface is rather full and rounded at the anterior end, flattening out posteriorly where, near the apex, it takes a rather sharp downward curve, Figs. 2 and 3, as though the point were slightly bent. Near the posterior end, the median dorsal margin forms a rather prominent shoulder, *s*, giving this portion of the appendage a characteristic contour.

The anterior end, which slopes diagonally forward and outward, is provided with a beautifully modeled articular condyle, *c*. It is a smooth, rounded prominence, flattened dorso-ventrally, slightly depressed on its anterior surface, and with a well defined constriction around its base. Its median end is continuous with a distinct ridge that extends along the middle of the median surface of the appendage, Figs. 1–3, *r*.

The entire dorsal surface of the joint was covered originally with a polished enamel like layer, similar in color and texture to that on the dorsal shield of Tremataspis. But a large patch of this layer, on that part of the specimen that originally protruded from the matrix, is worn off, thus exposing the hexagonal meshwork of vessels, filled with a reddish deposit, so characteristic of the middle layer of the shell of Tremataspis.

The polished outer layer terminates abruptly at the anterior end in a rounded edge that may be followed around the projecting anterior lateral angle, *p*. On the dorsal surface, this polished edge presents two well defined curves, a part of the posterior one being destroyed. On the ventral surface, the whole of the enamel layer is preserved, its sharply defined anterior margin forming three well defined rounded incisions, Fig. 1. The resemblance between what is left of the anterior enameled margin on the dorsal side, and the intact margin on the ventral, indicates that both were probably in the uninjured specimen quite similar.

The ventral surface of the appendage is perfect in every detail. In contour and texture it differs somewhat from that of the dorsal surface. It is slightly depressed in the middle, there are prominent thickenings on either margin, and the characteristic shoulder of the dorsal surface is absent. It is covered with coarse pits, the mouths of which look towards the distal end of the appendage as though they had at one time been occupied by coarse hairs directed backwards. This produces a surface texture quite different from the smooth surface on the dorsal side of the appendage.

When we look at the appendage from the median side, Fig. 2, its asymmetry is clearly seen. Unfortunately the characteristic texture of the median surface is not well shown in the photograph. This was due in part to the fact that the articulating condyle was accidentally broken off and the shiny surface of the cement used to repair it made it difficult to obtain good photographs. It shows, however, with sufficient distinctness that the enamel layer which covers only the posterior end of the median surface, abruptly terminates anteriorly in a thick fold, *me'*.

The remaining portion of the median surface is covered with a peculiar layer entirely different in texture from that on the dorsal and ventral surfaces. It is much darker colored and its lustreless surface, which is irregularly folded, is devoid of pores, except a few scattering ones of comparatively large size. It has the appearance of having been a tough flexible membrane that had become dried and wrinkled before fossilization. Nearer the anterior end, the conspicuous median ridge and the well moulded condyle indicate the presence of firmer bone-like tissues.

I regard the whole structure as the distal joint of an oar-like swimming appendage that served the same function for Tremataspis that the "pectoral appendages" do in Bothriolepis and Pterichthys. That we are dealing with a projecting appendage of some kind and not a superficial plate is shown by the presence of the polished outer layers of the shield on both surfaces ; and that it was freely movable, is shown by the prominent articular condyle at its anterior end.

We know with certainty that such a plate could not have been a mere spine attached to either the ends of the cornua, or to the lateral margins of the cephalic buckler back of the oral region, or to any part of the dorsal surface of the head, for on these parts, the structure of which is perfectly well known, there are certainly no articulating surfaces that could serve for the attachment of either spines or appendages of this character. We may also assure ourselves that it could not be a median dorsal or ventral spine of the trunk, for the difference in texture and contour of its two surfaces proves that it was a part, or the whole, of a paired organ. We are, therefore, limited to the assumption that it formed a part, or the whole, of a paired organ attached to the sides of either the trunk or to the anterior ventral part of the head.

The probable mode of attachment of the joint, and its direction of movement, is indicated by the sharp slope of its anterior end, the length of the process on its anterior lateral margin, and by the shape and condition of the condyle. These conditions indicate that the plate could not have been attached directly to the sides of the body, for in that case it would have to be directed diagonally backwards and the prominent anterior lateral process would prevent that range of forward and backward movement which the shape of the condyle clearly indicates it did have.

The same argument would preclude the possibility of its being attached *directly* to any of the marginal incisions in the oral region of the ventral surface. In a word, there is no place where there is any likelihood that such a structure could be attached directly to the body, and there is no structure known in the Ostracoderms with which it can be compared, if not with the distal joint of the pectoral appendages of Bothriolepis or Pterichthys. With this it corresponds fairly well except that it is formed of a single plate, instead of several.

We therefore assume that the plate in question formed the distal joint of an appendage something like that of Bothriolepis. It now remains for us to find the plates that make up the armor of the proximal portion of the appendages.

Basal joint: I regard the structure shown in Figs. 4 and 5 as one of these plates. Two specimens of this plate are in the collections at Dartmouth College; a nearly perfect one from which this photograph was made, and a fragment of another. One or more of these plates are also in the collection of the Imp. Acad. of St. Petersburg. The plate is 6 mm. long and 6 mm. wide.[1] It is roughly diamond shaped, but not quite symmetrical in outline, as the angle on the right side is higher and broader than that on the left. There is a corresponding differ-

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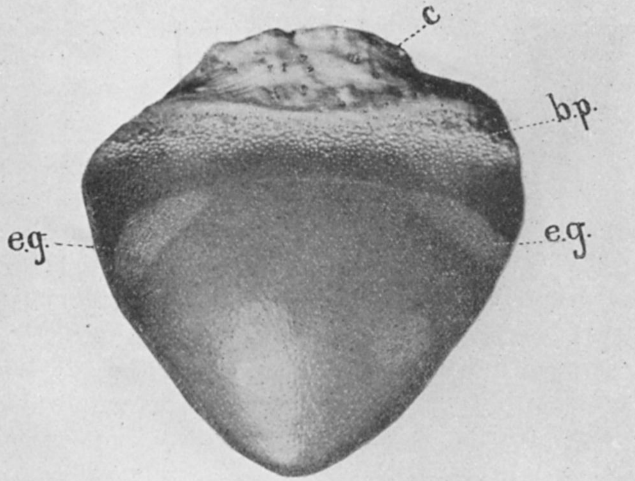
[1] Rohon makes his anterior median plate considerably smaller than this, namely 4 × 3 mm. This difference I am inclined to believe is due to the fact that his plate was imperfect, and not entirely exposed.



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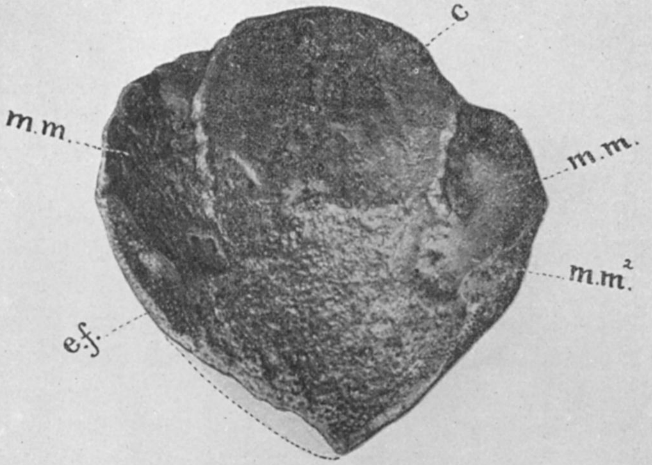

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FIG. 4. Basal plate of Cephalic appendage from dorsal surface. × 10.

FIG. 5. Same from inner, or visceral, aspect. × 10.

c. articular collar. *e.f.* fold of polished layer on the ventral side. *e. g'.* & *e. g.* groove cut into the polished surface layer. *m. m.* & *m. m.*^{2} muscle markings.

ence in the inner surface, showing clearly that *the plate is not bilaterally symmetrical.* What I shall call the distal portion of the dorsal side (Fig. 4) is strongly arched and has a very smooth, beautifully polished surface dotted with minute pores. It is a slaty gray color, becoming a dark chocolate on the left, in that part that was originally deeply imbedded in the matrix. The texture changes rapidly at the anterior end, where there is a broad band of coarse dimples in the polished floor of a shallow groove, *b. p.* In front of this groove the plate narrows to form a thick collar, *c*, very different in appearance from the rest of the plate. It is lighter colored and has a smooth, but irregular surface that lacks the brilliant polish and regularly distributed minute pores of the posterior part. It is provided with a few large openings irregularly distributed. The whole appearance of the collar suggests that it was made to fit into a nearly circular opening and that it was held in place there by stout ligaments attached to its roughened surface.

A remarkably clear cut, semicircular groove is seen on the beautifully polished and rounded surface of the plate a little way below the band of pores, *c. g.* It is seen on all the specimens examined (four in all) and must have been produced during the lifetime of the animal by a rotatory movement of the plate that brought it in contact with some hard object. The meaning of this groove will be considered farther on.

By the exercise of some care, the matrix was successfully removed from the inner surface of the plate, thus displaying a somewhat remarkable structure, Fig. 5. A small fragment of the edge of the plate was broken off in excavating the matrix, the outline of the missing portion being indicated by a dotted line. The plate is now seen to be of a uniform dark chocolate color and with a concave inner surface. The posterior half of the inner surface has a coarse rough texture different from that seen anywhere else in Tremataspis, but otherwise it shows no particular structure worthy of mention. In about the middle of either side, the margin is thickened and here the enamel layer of the outer surface extends a short distance on to the inner surface, *e. f.*

There are two large oblong depressions on either side (m. m.)

apparently made by the attachment of powerful muscles. The floor of each depression is irregularly ridged, and has a dull, almost shining, surface. At its posterior end is a still deeper rounded depression, m. m.,[2] that probably served for the attachment of a special group of muscle fibres. The rounded depression is considerably deeper and more clearly defined on the right side of the plate.

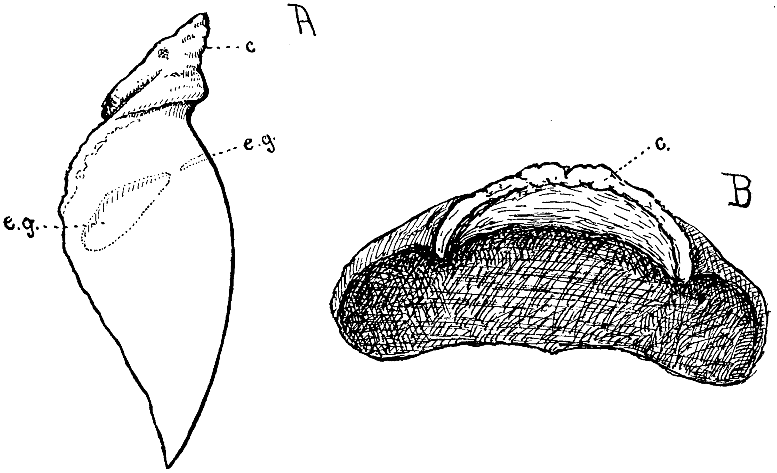

FIG. 6. Basal plate, A, from the side, B, from the anterior end. × 10.

The lateral margins of the collar that was seen on the outer surface, Fig. 4, *c*, extend about half way down the inner surface of the plate, forming a conspicuous ridge on either side of the muscle markings. When seen in profile from the anterior end, Fig. 6, B, the collar looks like a small concave plate adhering to the inner surface of the larger one. The concave inner side of the collar is smooth and undulating, but with a dull surface. It is provided with several large grooves leading to conspicuous apertures that evidently served for the passage of blood vessels to the interior of the plate. These grooves are instructive as they indicate that, as it stands in the figure, the blood vessels come to the plate from its upper end.

Rohon[1] has described a plate like the one we are now considering. His specimen was only partly exposed and he failed to see many important details. He looked on it as the anterior median oral plate. I have examined Rohon's specimen and there is no doubt that it is identical with the one in the Dartmouth collections. Rohon states, p. 188,

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[1] Zur Kenntniss der TrematGaspiden.

Mélanges Géologiques et Palæontologiques. *Bull. de l'Académie Imp. des Sciences de St. Petersbourg*, T. I. '94.

> "Die fur die erste Reihe von mir angenommenen zwei vorderen Seitenplatten sind am Original nicht allein zerbrochen, sondern auch gänzlich verschoben. Als die vordere Mittelplatte vermag ich nur vermuthungsweise die in den Figuren 12 und 13 a, b abgebildeten und isoliert gefundenen Platten ansprechen. Die Platten sind durch ihre bedeutende Wölbung ausgezeichnet; hingegen stimmen sie der Form und mikroskopischen Structur nach mit den ubrigen Platten vollkommen uberein. Dass jedoch die zwei vorderen Seitenplatten zu den nachfolgenden gehoren, dafur spricht sowohl ihre Lage wie ihre Beschaffenheit; sie sind ebenso an der Oberfläche glänzend und flach wie die meisten der nachfolgenden, wahrend die in deren Nähe sichtbaren Stücke von dem Umschlagsrande stark gewölbt und dünner erscheinen. Im Übrigen betrachte ich, wie gesagt, das Thatsächliche in Bezug auf die beiden vorderen Seitenplatten als etwas Unsicheres."

We must take exception to Rohon's statement that the so-called median oral plate agrees completely in form and microscopic structure with that of the remaining oral ones. In the Dartmouth specimens, the surface is very smooth and shining whereas in the cast of that specimen in St. Petersburg which shows nearly all the plates "in situ" the surface of the oral plates is broken into very delicate ripple marks similar to those usually seen on the dorsal and ventral surfaces of the buckler. Moreover, the isolated so-called median plate has rounded outlines and a strongly convex surface so that it would appear quite out of place among the true oral plates which have nearly straight line contours and flat surfaces.

The smooth surface texture of this plate may be a specific difference, as I have seen some specimens of Tremataspis with very thick, strongly arched bucklers and smooth surfaces. They appeared to belong to a different species from any of those already described. However, a small recently discovered isolated plate belonging to the oral region shows a smooth polished surface similar to that of our shield-shape plate, indicating that the surface texture of the oral plates may have been slightly different from that on the rest of the body.

Neither can I agree with Rohon's view that the oral surface of the St. Petersburg specimen which shows the oral plates *in situ* is so distorted as to force the median plate strongly to one side. As I have pointed out elsewhere the true anterior median oral plate is here almost exactly in its proper place, and it is very different in size and shape from the isolated one Rohon wrongly supposed to be a median oral plate.

The location of this shield shape plate in Tremataspis, for there can be no reasonable doubt that it belongs to this genus, has been a great puzzle. The objections to Rohon's view that it is a median plate lying just behind the mouth are overwhelming. It is (1) much too large. (2) It is asymmetrical and cannot be regarded as a median plate. (3) Its beautifully preserved structure is totally unlike a jaw which we must assume it to be if placed in that position. (4) The rounded collar at its anterior end, the two powerful and counteracting muscles attached to its inner side, and the sharply cut grooves on the polished outer surface, that were unquestionably worn by contact with some other hard part, shows conclusively that this plate was attached by the collar on its anterior surface to some circular opening and that it had a wide range of rotary movement from side to side, an improbable movement in a plate thus located.

The resemblance of this plate to the hypostoma of Trilobites in its shape, muscle markings and its probable mode of motion, led me at first to consider it as a preoral plate attached by its collar to the anterior ventral margin of the dorsal shield. But its asymmetry, which at first did not impress me so forcibly as it did later, its large size, and the lack of correspondence between the shape of its anterior margin and the anterior margin of the dorsal shield, gave little support to such an idea. If this plate belongs to the cephalic shield of Tremataspis, there is but one place remaining where it could have been attached and that is to the large anterior semicircular incision on the margin of the cephalic buckler, that is at the point where, on other grounds, we have reason to suppose that a pair of oar-like appendages were attached. Fig. 7. If we compare this plate, on this assumption, with the corresponding plate at the base of the appendage of Bothriolepis, as figured by Whiteaves, we see that they are indeed somewhat similar. Both plates have a strongly convex outer surface, a pointed posterior extremity and an articulating anterior margin. In Figs. 7 and 8 I have reconstructed the appendages of Tremataspis on the assumption that the basal portion was covered by several plates similar to those of Bothriolepis. In these figures the basal and distal parts of this hypothetical appendage and also, as far as possible, the marginal incision of the cephalic shield, are drawn to the same scale. I have described this incision in my first paper and have shown that it lies on the down turned margin of the shield. I assume that the collar of the basal plate with its convex side facing dorsally, was attached by ligaments, or a flexible membrane, to the margins of the incision, the membranes or ligaments being long enough to allow great freedom of movement. It is not likely that the collar of the basal plate actually fitted into the incisions, for its surface is not smooth enough, and if it did there could hardly be the requisite freedom of movement.

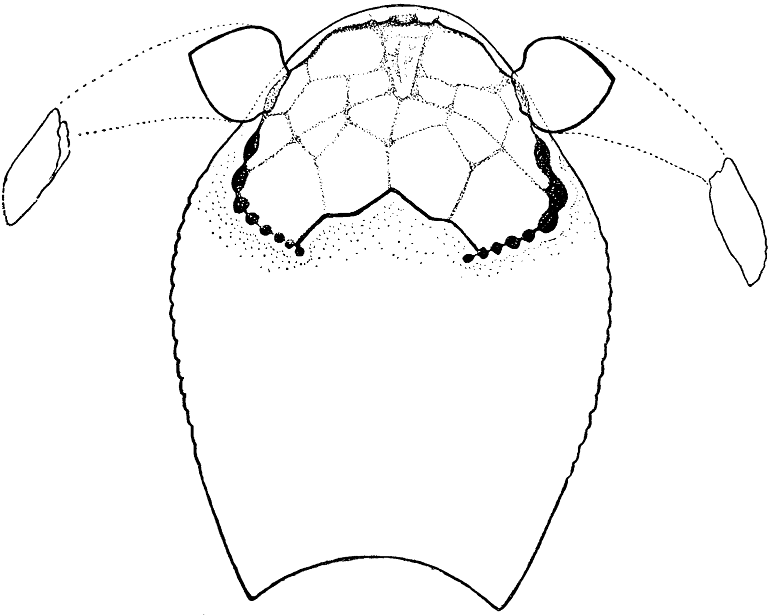

FIG. 7. Reconstruction of the ventral side of the head of Tremataspis, indicating the mode of attachment of the cephalic appendages. × 2.

It is clear that in the swimming movements of such an appendage, Fig. 8, the blade-like distal part would probably be carried upward and forward with the sharp cutting edge in advance, thus offering the least resistance. On the return stroke, which impelled the animal forward, the broad under surface would be

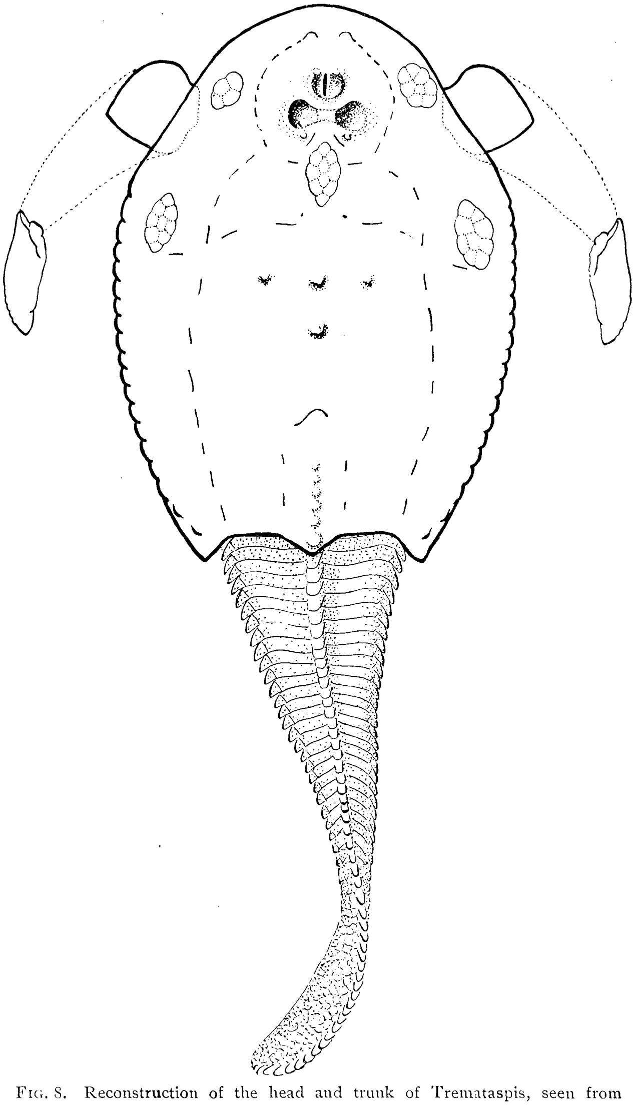

FIG. 8. Reconstruction of the head and trunk of Tremataspis, seen from above. × 2.

in advance the whole appendage swinging backwards and downwards. In performing a complete stroke, the apex of the appendage would describe either an ellipse or a fig. ∞, while at the beginning and end of each forward and backward stroke the appendage as a whole would rotate on its own long axis, through an angle of something like 45 degrees. These movements would cause the dorsal surface of the basal plate to strike, and rub against the folded margin of the dorsal shield, and would produce just such a series of grooves as are shown so clearly on the plate. These grooves are well worth careful consideration.

There are three grooves arranged in the arc of a circle just back of the band of coarse pores. On the left side of the plate, Fig. 4, *e. g.*' the groove has a symmetrically rounded floor, is perhaps a fifth of a millimeter deep, and narrows at either end till it disappears. The anterior boundary of the groove is more sharply curved than the posterior. The groove on the opposite side of the plate is less sharply marked, shallower than the first, and its anterior and posterior boundaries are alike. A very narrow hardly visible groove continues the lines of the first two so as to complete the arc of a circle, but it does not open directly into either of the two marginal grooves. These three grooves are apparently formed by friction against some hard object during the same movement, except that the contact seems to have been more forcible at the beginning and at the close of the movement. It will also be observed that these grooves do not lie on the most protruding *part of the surface* but in a kind of recess between the most prominent portion and the pitted anterior border, Fig. 6 *A*. It is clear therefore that the grooves must have been formed by contact with some narrow projecting rim and not by a broad flat surface. This is in harmony with our supposition that the grooves were formed by the rotation of the basal plate of the appendage against either the ventral margin of the cephalic shield or against the adjacent oral plates on the opposite side of the opening to which we have assumed the appendage was attached.

If one constructs a rough working model of an appendage such as I have described, it will be clear that as the appendage approaches the beginning or end of a stroke, it becomes more and more nearly parallel with the long axis of the head, the tendency being to draw the basal plate more and more diagonally across the margin of the shield, instead of straight across it as during the middle of the stroke. This factor and the sudden change in the intensity of muscular contraction at the beginning and end of each stroke furnish a very satisfactory explanation of the increased depth and width of the ends of the eroded groove.

To return to the basal plate shown in Fig. 4. A close examination of its convex surface shows a second belt, not shown by the photograph, farther back than the first where the surface enamel has been very slightly eroded. It extends about two thirds of the way across the lower portion and is coextensive with the line of greatest elevation of the surface. It is hard to see, on any supposition as to the location of the plate how this abrasion could have been produced by contact with any part of the animal's body to which the plate was attached. I assume that the abrasion, if made during the lifetime of the animal, must have been produced by contact with the bottom over which the animal was moving.

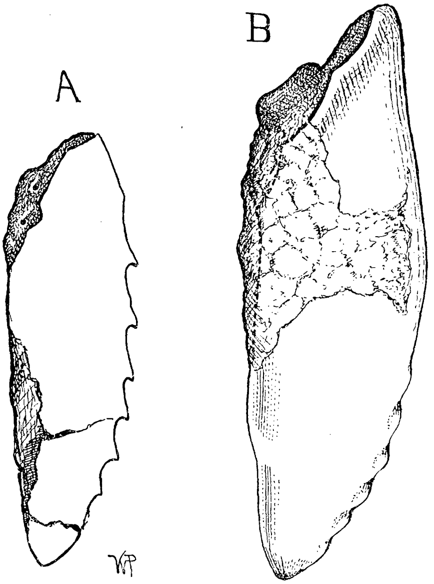

FIG. 9. Distal ends of two different cephalic appendages of Trematapsis, seen from the dorsal surface and drawn to the same scale. B shows the same plate shown in figs. 1–3. × 10.

Since writing the above description of the pectoral appendages of Tremataspis, a new specimen of the distal joint has come into my possession, Fig. 6 A. It is unquestionably of the same character as that shown in Fig. 3. It has the same general form and texture but differs from it in certain details. It is considerably smaller, measuring only 5.66 mm. in greatest length by 1.65 mm. in greatest width. There are six or seven very prominent marginal serrations or spines. The curvature of the dorso-median surface indicates the presence of the peculiar shoulder seen in Fig. 3, but the surface is broken along the edge where such a shoulder should be. The smooth anterior margin of the shining surface layer appears to have been straight instead of scalloped. There is the same peculiar wrinkled and lustreless surface on its median side, extending not quite to the distal end. At the proximal end, this layer forms an irregular prominent surface with two or three round openings for the passage of blood vessels, but without any trace of an articular condyle, or articulating surface, such as was seen in the first specimen. The surface at this point is intact, showing that an articulating surface could not originally have been present.

While there can be no doubt that the two structures in question are of the same nature, and that both belong to Tremataspis, the differences between them, in the above mentioned details, are so great that we can hardly regard them as identical. We are left then to the conclusions that (1) they are either homologous structures from different species of Tremataspis, against which it may be urged that the surface texture is the same in both and like that known in *T. schmidtii* only. (2) or they may be serially homologous structures from the same species. This conclusion harmonizes with the fact that both structures agree in surface texture but not in form, and with the fact that there is a series of marginal openings on the ventral surface serially homologous with the anterior ones to which the pectoral appendages are attached. I have already suggested that these openings indicated the presence of other appendages of a smaller size than the pectorals, although there was no evidence at that time available that furnished any hint as to what the character of these appendages might be. This fact we have always borne in mind in view of the great range in structure and function presented by such organs in other animals whose structure is better known than that of Tremataspis, and also in view of the fact that there is often such a great range of variation in a series of these organs in the same animal. Nevertheless in view of the above named consideration and while well aware of the uncertainties involved, it seems to me we must not lose sight of the possibility that there may have been more than one pair of jointed appendages in Tremataspis, similar to those described as pectorals, and that the fragment in question may have belonged to one of these additional appendages.

In conclusion, therefore, I believe that we are justified in the statement that Tremataspis is provided with a pair of oar-like swimming appendages similar to those of Bothriolepis and Pterichthys, and that similar appendages were probably present in Pteraspis, Cyathaspis and Tolypaspis.

In Tremataspis, these appendages were probably attached to the largest pair of incisions on the anterior ventral margin of the head. Appendages attached there would agree (1) in point of attachment with those in Bothriolepis and Pterichthys. (2) they would be attached to a part of the head best fitted, so far the shape of the head and the location of its centre of gravity is concerned, to serve as the support for a pair of swimming appendages. (3) There is no other part of the head to which such appendages could be attached. (4) They could not have been attached to the trunk, because the trunk of Tremataspis must have been of relatively small size, judging from the way the shield tapers posteriorly, from the small opening at the posterior end, and from what we know of the size of the trunk scales and of the size of the trunk in Thyestis and other Ostracoderms. It is therefore extremely improbable that large appendages could have been attached to a body so small that the centre of gravity must have been situated in the head, some distance in front of the anterior end of the trunk.

That by far the greater share of the work of locomotion in the Ostracoderms must have been performed by the oar-like cephalic appendages is indicated by their anterior position and great size in Bothriolepis and Pterichthys, and by the relatively small size of dorsal and caudal fins in the latter genus. Such a condition is in marked contrast to that in many of the most primitive of the true fishes where the pectorals are much smaller relatively, serving rather as balancers, the principal work of locomotion being performed by the tail and caudal fin.

Among true vertebrates, the only structures suggestive of the cephalic appendages of the Ostracoderms are the external gills during their early embryonic stages, including among these structures the "balancers" of Amphibian larvæ. The large size and anterior position of the latter appendages make them especially suggestive of the oar-like appendages of Tremataspis.

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